THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE
VII. SUMMARY AND CONCLUSIONS

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INTRODUCTION

IN PRECEDING numbers of this series (1–5, 10), we have described the floral and vegetative morphology of the Winteraceae. The data presented in these papers, together with Smith's (12, 13, 14) taxonomic treatments, provide the basis for a critical evaluation of available evidence regarding the composition, relationships, and phylogenetic significance of the family.

As now constituted, the family is composed of six genera: (1) *Drimys* J. R. & G. Forst., with 40 species in America (Mexico to Cape Horn and Juan Fernandez), Tasmania, Australia, New Guinea, Amboina, Celebes, Borneo, and the Philippines, (2) *Bubbia* v. Tiegh., with 30 species in New Guinea, Queensland, New Caledonia, and Lord Howe Island, (3) *Belliolum* v. Tiegh., with 8 species in New Caledonia and the Solomon Islands, (4) *Pseudowintera* Dandy, with 2 species in New Zealand, (5) *Exospermum* v. Tiegh., with 2 New Caledonian species, and (6) *Zygogynum* Baill., with 6 species in New Caledonia. The number of species in each genus, as outlined above, will doubtless be subject to future revision, since it is probable that the family will gain new members, especially in the genera *Drimys* and *Bubbia,* as the exploration of New Guinea progresses. The family now contains about 88 species, and one may anticipate that this number will eventually be increased to well over 100. The Winteraceae, therefore, instead of being the small group which only recently was dismissed as an inconsequential appendage of the Magnoliaceae, are seen to be a family of considerable consequence both in size and in geographic extent.

MORPHOLOGICAL CHARACTERISTICS

The Winteraceae are characterized as a family by their distinctive pollen, vesselless xylem, and curiously occluded stomata, and by combinations of cauline, floral, and foliar characters that are not duplicated in other dicotyledonous families.

XYLEM. The xylem of the Winteraceae is of a structurally unique type among extant representatives of the angiosperms, the woods even of the similarly vesselless *Trochodendron* and *Tetracentron* having significant differences in their rays, wood parenchyma, and other structural features. Although the xylem of the Winteraceae is distinctive, it exhibits certain trends of structural specialization within the family, leading for example toward reduction or elimination of wood parenchyma in Sect. *Wintera* of *Drimys,* toward excessively widened multiseriate rays in *Pseudowintera,* and toward reduction of cell size, particularly in dwarfed or microphyllous species, in Sect. *Tasmannia* of *Drimys.*

LEAF. The lower epidermis of winteraceous leaves is characterized by having a more or less extensive alveolar modification of the cuticle which differs from the waxy layers of other angiospermic leaves, in its higher melting point and insolubility in boiling alcohol, hot ether, and other non-polar solvents. The alveolar material forms more or less massive deposits in the oval or circular depressions in which the stomata are situated, covering the guard cells and occluding the orifice. Although "plugged" stomata have been reported, Wulff (17), in various monocotyledons and dicotyledons, the particular morphological and chemical expressions of the phenomenon in the Winteraceae appear to be distinctive of the family.

The mode of insertion of the foliar vascular tissue in the eustele is stereotyped and stable throughout the Winteraceae, being prevailingly of the so-called trilacunar type. On the contrary, the patterns of vascularization within the petiole and lamina are diverse and variable within certain specific limits. Two trends of specialization are discernible in *Drimys,* leading (1) toward division of three foliar strands to form more or less numerous derivative bundles, and (2) toward fusion of foliar strands to form a single arc-shaped vascular bundle. The former trend of specialization is intensified in *Belliolum* and *Bubbia* and attains its climax in *Exospermum* and *Zygogynum.*

INFLORESCENCE. The inflorescences of the Winteraceae exhibit a wide range of morphological variability. In *Drimys* they are clearly axillary or intercalary on monopodially elongating axes, whereas in *Bubbia, Belliolum, Exospermum,* and *Zygogynum* they are terminal or "pseudoterminal" on sympodially elongating shoots. In *Pseudowintera* the inflorescences are apparently terminal or "pseudoterminal" on sympodial axillary short shoots of a monopodially elongating vegetative axis. The individual inflorescences of different representatives of the family exhibit numerous transitions between complexly branched, many-flowered, cyme-like types and single-flowered ones that may be either axillary (*Drimys*) or terminal (*Zygogynum*). These numerous transitional types of inflorescences are suggestive of phylogenetic series either of reduction or amplification.

According to Parkin (11), the pseudoterminal inflorescences of such genera as *Bubbia* and *Belliolum* developed from an intercalary type by the abortion of the terminal bud. In other words, a group of axillary inflorescences is congested at the apex of the stem, and the structure as a whole appears to be terminal because the apical bud is suppressed or absent. It should be emphasized in this connection, however, that if the pseudoterminal inflorescences of *Bubbia, Belliolum, Exospermum,* and *Zygogynum* are derived from intercalary ones as of *Drimys,* the terminal single flowers of certain species of *Zygogynum* must represent the end of a reduction series. There is much in the comparative morphology of the Winteraceae as a whole to justify such a conclusion.

PERIANTH. The flowers of the Winteraceae are characterized by having a combination of gamosepaly and polypetaly, together with a strong tendency toward reduction in the number of constituent parts both of the calyx and corolla. Variations in the number, size, form, and texture of the petals are of specific rather than generic significance. On the contrary, the calyptrate calyx of *Drimys* serves to differentiate this genus from the other genera of the family, which have rotate or variously lobed calyces that do not enclose the buds.

STAMENS. The microsporophylls of the Winteraceae are of three distinct morphological types. Four of the genera, *Bubbia, Pseudowintera, Exospermum,* and *Zygogynum,* have short, comparatively broad, more or less truncated or apically flaring microsporophylls. The more or less protuberant sporangia are attached to the broad apex of these sporophylls and are oriented either transversely or in various diagonal positions. *Belliolum* is characterized generically by having apically tapered microsporophylls and particularly by having laterally attached sporangia oriented parallel to the long axis of the sporophyll. In these five genera, the sporophylls are not differentiated into filament, anther, and connective, and the sporangia are not excessively protuberant. The microsporophylls of *Drimys* fluctuate considerably in length and breadth, not only in different species, but also within the same flower. They are characterized, however, by having markedly protuberant thecae that are attached to the much constricted upper part of the sporophyll. The microsporophylls of Sect. *Wintera* are relatively broad, but those of Sect. *Tasmannia* are at times much elongated and narrow. The latter are more typically stamineal, exhibiting differentiation into filament, connective, and anther. Our comparative investigations of microsporophylls in other ranalian families suggest that there are two trends of morphological specialization in the Winteraceae, leading in *Bubbia, Pseudowintera, Exospermum,* and *Zygogynum* to the formation of broadly truncated sporophylls bearing transversely oriented apical sporangia, and in *Drimys* to apically constricted sporophylls bearing markedly protuberant, laterally attached, subapical sporangia.

POLLEN. Throughout the family the pollen is associated at anthesis in permanent tetrahedral tetrads, each pollen grain having a distally oriented germ pore and a characteristically reticulate exine, the reticulations being composed of more or less extensively coalesced rods. The tetrads are unlike those of the Lactoridaceae and of certain representatives of the Annonaceae, Monimiaceae, and Nymphaeaceae, and are morphologically unique among families of ranalian affinities. Two obvious trends of specialization in pollen morphology are discernible, however, within the Winteraceae, leading to the formation of (1) a minutely, rather than a coarsely, reticulate exine in *Exospermum* and *Zygogynum,* and (2) in Sect. *Wintera* of *Drimys,* tetrads having four conspicuously protuberant papillae when dried pollen is re-expanded in water or lactic acid.

CARPELS. The salient trends of carpellary specialization within the Winteraceae are distinct and obvious. The carpels of Sect. *Tasmannia* of *Drimys* are conduplicate megasporophylls having a stipe and an adaxially folded lamina, with a deep slit-like opening that extends inward to the longitudinally oriented locule. The free margins and adjacent surfaces of the open conduplicate megasporophyll are provided with glandular hairs. In other words, the carpels have conspicuous stigmatic crests (actually double) which extend from the region of the stipe along the conduplicate adaxial parts of the sporophyll and slightly overtop its apex. When spread open, the lamina exhibits a palmately 3-veined vascularization, and the more or less numerous anatropous ovules are attached in longitudinally oriented series between the dorsal and ventral veins. The ovules are vascularized in part by short branches of the two ventral veins, in part by branches of the dorsal vein, and in part by strands originating near anastomoses of the ventral and dorsal vascular systems, the proportions of the three types of vascularization fluctuating from carpel to carpel. Thus, the ovules are attached not to the margins, but to the adaxial surface of the lamina of the megasporophyll.

The carpels throughout Sect. *Wintera* of *Drimys* have a fundamentally similar conduplicate form, vascularization, and placentation, but the external stigmatic crests are restricted to the adaxially projecting subapical part of the megasporophylls. The approximated ventral surfaces of the conduplicate carpels are firmly concrescent except at the level of the stigmatic crests, and therefore the megasporophylls cannot be unfolded as in the case of the less modified sporophylls of Sect. *Tasmannia*. In other words, with the closure of the cleft-like opening, the conduplicate carpels retract and eventually eliminate the stigmatic crests from the sealed parts of the megasporophyll. Thus, the subapical projection of the Sect. *Wintera* type carpel is not to be interpreted as a style-like outgrowth, but rather as a persistent remnant of the extensive adaxial stigmatic crests of open megasporophylls of the Sect. *Tasmannia* type.

Various transitional stages in the closure of conduplicate megasporophylls and in the restriction of their stigmatic crests occur in *Bubbia*, but in this genus, as in *Belliolum*, *Pseudowintera*, *Exospermum*, and *Zygogynum*, there is in addition a more or less pronounced abaxially directed deformation of the conduplicate megasporophylls. These trends of specialization commonly lead to the formation of carpels having conspicuously broadened and flattened apices with restricted, more or less transversely oriented, and therefore apparently terminal stigmatic crests. In such carpels there are concomitant modifications in the form and orientation of the locule, in the placental surfaces, and in the vascularization of the deformed conduplicate megasporophylls. Owing to these concomitant deformations from longitudinal to curved or transverse orientations, it is evident that the apparently terminal parts of the carpels actually are homologues of the ventral parts of primitive conduplicate megasporophylls of the Sect. *Tasmannia* type. The true apex of the carpel is curved around into a dorsal position. In the case of the syncarpous species of *Zygogynum*, the abbreviated stigmatic crests and the placentation appear to be dorsal. This is due, however, to the fact that a morphologically ventral part of the concrescent sporophylls has been deflected into an abaxial orientation and thus overtops the shortened morphologically dorsal part of the carpel.

VASCULARIZATION OF BRACTS, BRACTEOLES, AND FLORAL APPENDAGES. As previously stated, the vascularization of leaves in the Winteraceae is diversified and variable except in their trilacunar nodal attachments, which are stereotyped and stable throughout the family. In the case of fertile axes, even the vascular attachments of the appendages exhibit more or less extensive ranges of variability. Bracts and bracteoles may have three traces or the vascular strands may be reduced to one. Similarly sepals and petals may have three traces or the traces may be reduced to one or amplified to more than three. Each stamen has a single trace, but its mode of attachment to the toral vascular system is diversified and variable. The carpels may have a concentric or crescent-shaped trace, such as not infrequently occurs in petioles, or three traces, or the traces may be reduced to two or amplified to more than three. Accompanying this diversification of trace number and trace insertion is the occurrence in the flower of an irregular, variable, and complex eustele, which is due to an anastomosing and branching of bundles and the non-association of certain interfascicular regions with traces. The ranges of structural variability within species or genera may or may not overlap. Much additional material must be analyzed, however, before patterns of vascularization, either of the leaf or flower, can be utilized as a basis for sound taxonomic generalizations within the Winteraceae.

COMPOSITION OF THE WINTERACEAE

Various extraneous genera have in the past been assigned to the Winteraceae. All of these with the exception of *Illicium* have subsequently been transferred to more appropriate families. That *Illicium* should be segregated from *Drimys* and its allies and placed in an independent family has been suggested by van Tieghem (15), Diels (8), and McLaughlin (9). There is ample justification for such a procedure. The genus exhibits none of the distinctive characteristics of the Winteraceae and there are no significant similarities in any part of the plant that may be interpreted as indicative of close relationship to *Drimys* and its allies. The pollen is of a fundamentally different structural form, being typically tricolpate. Not only are there numerous vessels in the secondary xylem, but also the multiseriate rays are of a highly modified and much reduced type. The primary vascular cylinder of the stem is of a continuous pseudo-siphonostelic rather than a discontinuous eustelic type. The nodal anatomy and vascularization of the leaf are of a fundamentally different form, being unilacunar instead of characteristically trilacunar. The stomata are not occluded as in the Winteraceae and are of a distinctive morphological type, as are the structural patterns of the cuticle. The vascularization patterns of the torus and floral appendages are unlike those encountered in *Drimys* and its allies. Furthermore, the specializations of the conduplicate megasporophylls have progressed along fundamentally dissimilar lines, leading (1) to constriction of the apical part of the sporophyll and the formation of a style with "decurrent" stigmatic crests, and (2) to reduction of the ovules to one and its localization in the closed, more or less extensively adnate, basal part of the conduplicate carpel. The calyx is polysepalous, never rotate or calyptrate, and the stamens are of different morphological form. The chromosomes, as Whitaker (16) has shown, differ in size, form, and basic number from those of the Winteraceae. Although *Illicium* is not closely related to *Drimys* and its allies, it exhibits a number of significant similarities to the Schisandraceae. Whether the genus should be included in this family or segregated in an independent family, Illiciaceae, as suggested by van Tieghem (15) and Diels (8), is a problem which will be discussed in detail in a subsequent paper.

With the exclusion of *Illicium,* the Winteraceae become a homogeneous, natural aggregation of obviously closely related plants. The extant representatives of the family exhibit varying combinations of relatively primitive and highly specialized morphological characters, and the surviving genera in all probability represent end products derived from a common ancestry. There are two distinct categories of these genera: (1) *Drimys,* having intercalary inflorescences, calyptrate calyces, normally developed conduplicate carpels, and more stamineal appearing microsporophylls, and (2) *Bubbia, Belliolum, Pseudowintera, Exospermum,* and *Zygogynum,* having terminal or "pseudoterminal" inflorescences, rotate or lobed calyces which do not enclose the buds, carpels which exhibit more or less pronounced abaxial deformation, and microsporophylls that are not typically differentiated into filament, anther, and connective. Within the second category of Winteraceae, *Pseudowintera* is characterized by having terminal or "pseudoterminal" inflorescences on sympodial short shoots and by its much modified and excessively widened multiseriate rays, *Zygogynum* by its strongly developed syncarpy, and *Belliolum* by its apically tapered stamens, which bear laterally attached, longitudinally oriented sporangia, instead of transversely or diagonally oriented ones on a broad apex, as is the case in the other four genera of this category of the Winteraceae. The carpels of *Exospermum* are closely appressed and coherent at anthesis, as in certain species of *Bubbia,* but they are not actually concrescent or syncarpous as in *Zygogynum.* The diffused placentation, highly specialized foliar vascularization, and pollen, which is of the *Zygogynum* type, present serious obstacles to the inclusion of *Exospermum* in *Bubbia* as at present constituted. It should be noted, however, that available collections of *Bubbia, Belliolum, Exospermum,* and *Zygogynum* are so inadequate and the possibilities of additional representatives in unexplored regions so strong that these generic outlines may need future revision.

The Winteraceae are hermaphroditic with perfect flowers except in Sect. *Tasmannia* of *Drimys,* where the plants are dioecious or polygamo-dioecious, the staminate flowers usually bearing sterile carpels and the pistillate flowers being with or without functional stamens. The fertile carpels of Sect. *Tasmannia* (as of certain species of *Bubbia*) are, however, of a more primitive type than the obviously much modified conduplicate megasporophylls of Sect. *Wintera* of *Drimys.* The two sections of *Drimys* also exhibit more or less significant differences in their pollen, foliar sclerenchyma, and secondary xylem.

It is evident that Sect. *Wintera* of *Drimys* cannot have developed directly from Sect. *Tasmannia* or vice versa. In other words, both sections of *Drimys* must have been derived from much less specialized and now extinct ancestral groups. *Bubbia, Belliolum, Pseudowintera, Exospermum,* and *Zygogynum* are obviously more closely related one to another than any one of them is to *Drimys.* Although *Belliolum, Pseudowintera, Exospermum,* and *Zygogynum* may have developed from *Bubbia*-like ancestors, the five genera cannot be derived directly from *Drimys* or vice versa; they must have diverged from earlier and more primitive Winteraceae, from which the two sections of *Drimys* likewise were independently differentiated.

RELATIONSHIPS

In the past, *Drimys* and its presumed allies, including *Illicium,* have frequently been placed in the Magnoliaceae in a special tribe (Illicieae DC., Wintereae R. Br.) or subfamily (Drimyoideae Harms, Drimydoideae Skottsb.). However, to include such morphologically dissimilar elements as the Winteraceae, *Illicium,* the Schisandraceae, and *Tetracentron* in the Magnoliaceae broadens the concept of this family even beyond the limits of a natural sub-order. The evolutionary gap between the vesselless xylem of the Winteraceae and the relatively highly specialized vessel-bearing wood of *Magnolia, Liriodendron,* and allied genera is so great as to preclude any close degree of relationship between the two groups of plants. In addition, there are fundamentally significant morphological differences in the pollen, stamens, carpels, perianth, secondary phloem, nodal anatomy, vascularization of the leaf, stomata, patterns of vascularization of the torus and floral appendages, etc. Furthermore, the reported similarity (Whitaker, 16) in the basic chromosome number, i.e. 19,[1] is not indicative necessarily of close relationship, since the same basic number occurs in such diverse ranalian plants as *Trochodendron, Tetracentron,* and *Cercidiphyllum.*

As we have previously shown (6, 7), the Degeneriaceae, Himantandraceae, and Magnoliaceae (sensu stricto) form a compact natural group within the Ranales, the three families being more closely related to each other, on the basis of important morphological characters, than any one of them is to other families. The Winteraceae exhibit no significant evidence of close relationship to this group of families, even the salient trends of carpellary specialization being entirely different. The similarity between the carpels of *Degeneria* and of Sect. *Tasmannia* of *Drimys* is apparently due to the retention of primitive ranalian megasporophylls by plants which exhibit fundamentally different trends of morphological specialization in their flowers, stems, and leaves. Similarly, the vesselless xylems of the Winteraceae, *Trochodendron,* and *Tetracentron* should be interpreted as retentions of primitive vesselless types of ranalian wood by plants which show diverse trends of specialization in their other vegetative characters and in their reproductive organs. Too much emphasis has been placed in the past upon the mere fact that these plants are vesselless, without due regard to significant structural differences in their xylem. This will be discussed in greater detail in subsequent papers dealing with *Trochodendron* and *Tetracentron*.

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[1] The chromosomes of only one of the 88 species of Winteraceae have been studied. In "*Drimys Winteri*" the 2n number is ±76, but this hardly provides a basis for generalization concerning the family as a whole.

Thus, although the Winteraceae obviously are of general ranalian affinities, as evidenced by their secretory cells and other characters, they do not appear to be closely related to any specific surviving family of the ranalian complex.

PHYLOGENETIC SIGNIFICANCE

In the recently described (7) monotypic ranalian family Degeneriaceae, both the stamens and the open carpel appear to be primitive, palmately 3-veined sporophylls of but slightly modified form. The lamina of the megasporophyll is adaxially folded or conduplicate and bears numerous ovules on its morphological upper surface, between its dorsal and ventral veins. In other words, the ovules are not attached to the margins of a classical involute, sealed sporophyll, but to the ventral surface of the megasporophyll as in certain of the Cycadofilicales. The microsporophylls, as in the related Himantandraceae (6), resemble the sterile sporophylls ("staminodia") and are not differentiated into filament, anther, and connective. The two pairs of slender, vertically elongated sporangia are immersed beneath the abaxial surface of the sporophylls and are situated between the median and lateral veins.

The Winteraceae are particularly significant in the study of the comparative morphology and phylogeny of the dicotyledons, not only owing to their retention of a primitive vesselless xylem, but also owing to their retention of extensive transitional series of carpellary structures illustrating successive stages in the closure and morphological modification of primitive, open, conduplicate megasporophylls of the *Degeneria* type. In addition, there are within the family successive steps in the development of more typical stamineal structures which arise apparently by the reduction of broad microsporophylls to slender filament and connective and by concomitant emergence or protuberance of the microsporangia, i. e. thecae. Furthermore, the family exhibits numerous transitions between complex intercalary or "pseudoterminal" inflorescences and simple, single-flowered ones. Since the single terminal flowers of *Zygogynum* appear to be the culmination of a reduction series, it is a question whether the single, large terminal flowers of *Magnolia* may not have originated through similar reductions of a complex ranalian inflorescence. In any case, it is unfortunate that so much attention has been focused upon the Magnoliaceae (sensu stricto) in discussions concerning the origin of the angiosperms, for the seedlings, stems, roots, leaves, stamens, and carpels of these plants all exhibit a relatively high degree of morphological specialization. More primitive and significant ranalian structures are retained by such families as the Winteraceae, Degeneriaceae, Himantandraceae, Trochodendraceae, etc. It should be emphasized in this connection, however, that each of these families exhibits a combination of primitive and more or less specialized characters, indicative of reticulate rather than linear relationships and of common origin from an ancestral ranalian stock. Until essential fossilized material is discovered, the composite structure of such ancestors can be synthesized only by combining the more primitive features of a number of diverse families.

There is no known species or genus of the Winteraceae, either extant or fossil, from which the rest of the family may have been evolved. Each known surviving member of the family exhibits one or more trends of morphological specialization which exclude any possibility of the plant being ancestral to all of the others. The Winteraceae are obviously an extremely ancient group of dicotyledons, the surviving representatives of which are end products derived from a common ancestry. Many structural features of this hypothetical ancestry can be synthesized from extant species and genera with a high degree of certainty, whereas others must remain for the present more or less speculative or problematical. The following is our concept of such an ancestral winteraceous stock and of its salient trends of morphological specialization:

HABIT. Trees or large shrubs. Salient specialization: dwarfing of the entire plant or of its leaves, particularly in certain species of Sect. *Tasmannia* of *Drimys.*

XYLEM. Vesselless, with diffuse parenchyma and primitive heterogeneous type I rays. Tracheids large, extremely elongated and provided with a relatively high ratio of scalariform and multiseriate-bordered pitting. Salient trends of specialization: (1) reduction or elimination of wood parenchyma in Sect. *Wintera* of *Drimys,* (2) excessive broadening of multiseriate rays in *Pseudowintera,* and (3) reduction in tracheary size and pitting, particularly in dwarfed and microphyllous species of Sect. *Tasmannia* of *Drimys.*

LEAF. Simple, entire, glabrous, exstipulate, pinnately veined, having numerous ethereal oil cells, characteristically occluded stomata, and three separate traces with trilacunar nodal attachments. Most significant trend of specialization: increasing complexity of vascularization patterns in *Bubbia* and *Belliolum,* culminating in *Exospermum* and *Zygogynum.*

INFLORESCENCE. Plants hermaphroditic, with perfect flowers. Inflorescences probably complex and intercalary, as in Sect. *Wintera* of *Drimys.* Chief trends of specialization: (1) establishment of dioecious or polygamo-dioecious habit in Sect. *Tasmannia* of *Drimys,* (2) transitions from intercalary to "pseudoterminal" and terminal inflorescences, and (3) reduction of complex inflorescences to simple single-flowered ones.

CALYX. Gamosepalous, with a variable number of lobes. Salient trends of specialization: (1) reduction in the number of partly concrescent sepals to two, as common in *Drimys* and *Pseudowintera,* (2) elimination of the lobes to form entire or rotate calyces, and (3) complete concrescence of sepals to form a calyptrate calyx, as in both sections of *Drimys.*

COROLLA. Polypetalous, with an indefinite number of free petals. Chief trend of specialization: reduction in the number of petals, frequently to two (rarely to one or none) in Sect. *Tasmannia* of *Drimys*.

STAMENS. Numerous, sporophyll-like, and not differentiated into filament, anther, and connective, the sporangia partly embedded in the lamina of the microsporophyll. The exact form of the ancestral microsporophyll is uncertain. If the stamens of *Belliolum haplopus* (Burtt) A. C. Sm. and *B. Pancheri* (Baill.) v. Tiegh. are the least modified of surviving Winteraceae, as seems possible from comparative studies of other ranalian families, then there are two distinct trends of specialization in winteraceous microsporophylls, leading (1) in *Bubbia, Pseudowintera, Exospermum,* and *Zygogynum* to the formation of broadly truncated sporophylls bearing transversely oriented apical sporangia, and (2) in *Drimys* to more typically stamineal structures exhibiting various incipient stages of differentiation into filament, anther, and connective.

POLLEN. In tetrahedral tetrads, each grain having a distally oriented germ pore and a coarsely reticulate exine. Most significant trend of specialization: the development of a minutely reticulate exine in *Exospermum* and *Zygogynum*.

CARPELS. Sporophyll-like, stipitate, with conduplicate, palmately 3-veined lamina, having two closely approximated stigmatic crests which extend from the region of the stipe to the apex of the adaxially folded lamina, and bearing numerous anatropous ovules in two longitudinally oriented series between the dorsal and ventral veins, the ovules vascularized at least in part by branches of the dorsal vein. Chief trends of specialization: (1) reduction of the number of carpels, (2) closure of the megasporophyll with concomitant restriction of the stigmatic crests, (3) abaxial deformation of the megasporophylls with concomitant modification in the form and orientation of the stigmatic crests, locules, placentation, and vascularization, and (4) development of syncarpy in *Zygogynum*.

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